SOME SUGGESTIONS REGARDING THE SIGNIFICANCE OF CHLOROPLAST DNA VARIATION IN THE ASTERACEAE.

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Recent discoveries of a unique inversion in chloroplast DNA in most Asteraceae has led to some speculation on a possible ancient evolutionary split in the family. The data involved offers interesting reenforcement for some ideas that have been developing during recent decades, but some detailed suggestions seem to conflict with structural evidence of relationships within one tribe involved, the Mutisieae. A slightly altered view is offerred here along with the suggestion of a possible correlated evolutionary factor in the chemistry of the plants.

Jansen and Palmer (1987) describe an inversion in the chloroplast DNA of most Asteraceae that is unique to that family and which differs from the evident original form seen in other Dicotyledonous families. The families lacking the inversion are listed by Jansen and Palmer as Apiaceae, Araliaceae, Brunoniaceae, Campanulaceae, Caprifoliaceae, Dipsacaceae, Goodeniaceae, Rubiaceae, Stylidiaceae, Valerianaceae, in addition to the Solanaceae. In contrast, 15 tribes or groups treated as tribes of the Asteraceae show only the inverted form of the chloroplast DNA in all of their genera tested by Jansen and Palmer: Arctoteae (3 genera); Cardueae (3 genera); Lactuceae (3 genera); Liabeae (2 genera); Vernonieae (4 genera); Eupatorieae (3 genera); Heliantheae (8 genera including 2 Tageteae); Anthemideae (5 genera including Cotula and Ursinia); Astereae (5 genera); Calenduleae (3 genera); Inuleae (3 genera); and Senecioneae (3 genera). The interest centers on the tribe Mutisieae where three of the subtribes have the inversion: Gochnatiinae (4 genera); Mutisiinae (5 genera); Nassauviinae (3 genera); while one subtribe lacks the inversion: Barnadesiinae (3 genera). In its lack of the inversion, the Barnadesiinae is like the other Dicotyledonous families, and an obvious initial conclusion places that subtribe at the base of the evolution of the presently known Asteraceae. There is no reason to doubt the validity of the findings of the DNA inversion by Jansen and Palmer, but there might be a question regarding the full extent of their evolutionary conclusions.

The general suggestion by Jansen and Palmer (1987) that something in the Mutisieae is primitive within the Asteraceae finds support in other studies of the family. For decades the field has been progressing from the crude assumption that the Heliantheae is the primitive group in the family (Cronquist 1955). Carlquist (1961) was first to suggest that the Mutisieae were at least coequal with the Heliantheae as a primitive element of the Asteraceae. Poljakov (1967) placed the series of tribes containing the Heliantheae, now known as the Asteroideae, in a more derived position in the family while the tribes including the Mutisieae, now known as the subfamily Cichorioideae, were shown as more primitive. Robinson (1981) has gone on to show that the Heliantheae are not even the primitive tribe in the subfamily Asteroideae. Skvarla et al. (1977) noted that the pollen of the Mutisieae differed from that of most Asteraceae and most closely approached pollen of the probably rather closely related family Calyceraceae. Jeffrey (1977), in the same volume, noted the zygomorphic corolla form in the Mutisieae that caused him to regard the tribe as closest to the primitive form in the family. The findings of Jansen and Palmer (1987) reenforce this already growing body of evidence for primitiveness of the tribe.

The problem of the evolutionary interpretation of Jansen and Palmer (1987) arises from the assumption that the one subtribe of the Mutisieae, the Barnadesiinae, is actually so divergent from the remainder of the Mutisieae that all the other Cichorioideae and all the Asteroideae could have arisen from within the evolutionary gap (Fig. 1). The three genera of the Barnadesiinae tested, Barnadesia, Chuquiraga, and Dasyphyllum indeed have some odd characteristics. Dasyphyllum has no apical appendage on the anthers, a feature in contrast with the well-developed appendage characteristic of most Mutisieae. Nevertheless, Barnadesia and Chuquiraga of the same subtribe have an ordinary Mutisian apical appendage. Barnadesia seems almost unique in the whole subfamily Cichorioideae in the lack of spurred bases on the thecae of the anthers, but spurs like those of other Mutisieae are found in the subtribe in Chuquiraga and Dasyphyllum. Barnadesia is also unusual in the Mutisieae in the lophate form of its pollen (Fig. 2), but pollen of Chuquiraga (Fig. 3) and Dasyphyllum is much like that found in other subtribes of the Mutisieae (Fig. 3). The foregoing characters are mixed in the Barnadesiinae with every unique character matched by an opposite condition within the subtribe.

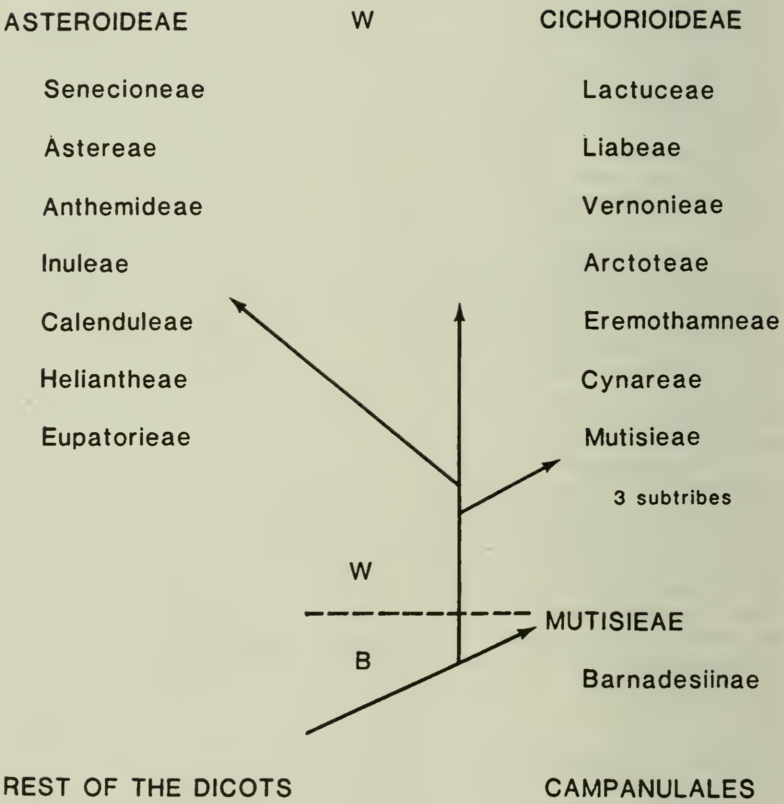

Figure 1. Evolution of Asteraceae following proposal of Jansen and Palmer (1987). Groups below dashed line (B) with uninverted chloroplast DNA. Tribes above dashed line (W) with inverted chloroplast DNA.

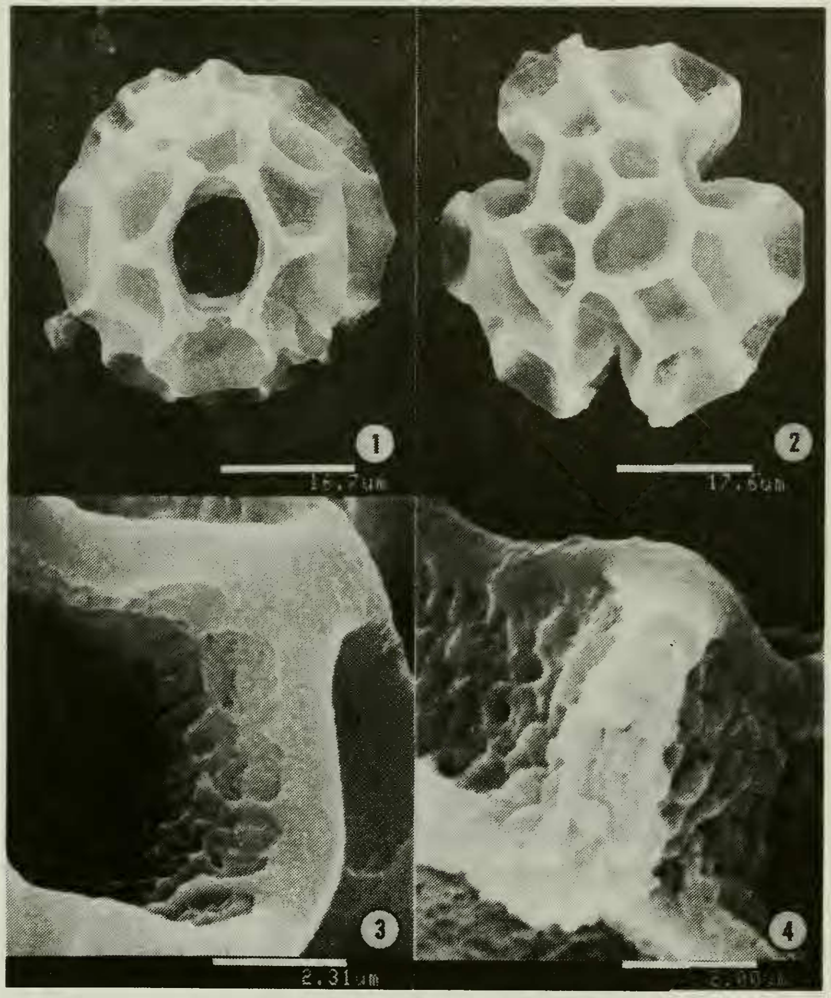

Figure 2. Barnadesia horrida Muschler. Pollen. 1. Colpar view. 2. Polar view. 3. Detail of crest. 4. Broken section of crest.

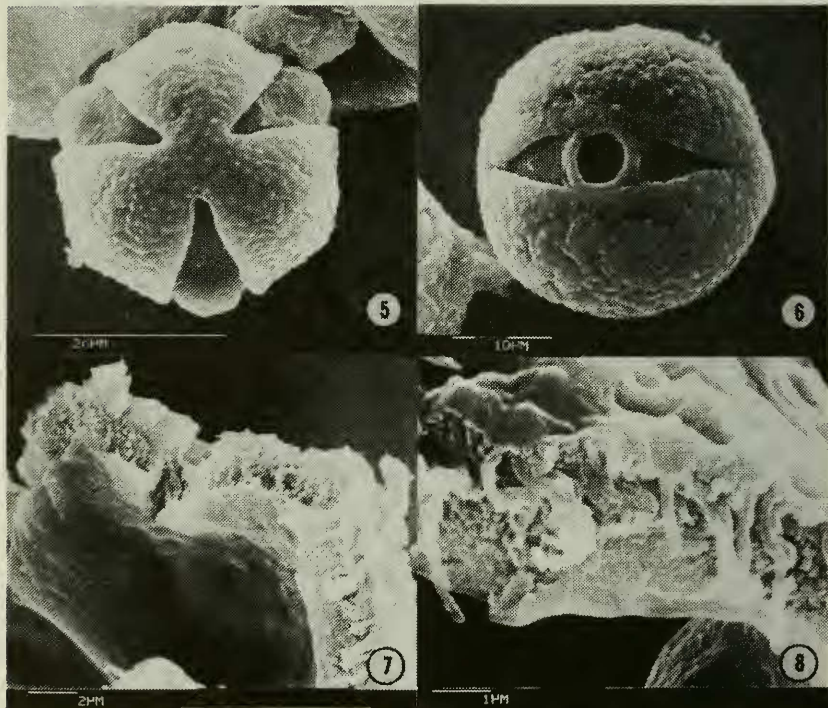

Figure 3. Chuquiraga jussieui Gmel. Pollen. 5. Polar view. 6. Colpar view. 7, 8. Broken edges of grains. Photographs of pollen prepared by Smithsonian Museum of Natural History SEM Laboratory. The microscope operated by Suzanne Braden. Stubs prepared by Mary Sangrey using facilities of Department of Botany Palynological Laboratory.

One is not inclined to believe that the Barnadesiinae are so remote from other Mutisiinae that the remainder of the Asteraceae could evolve from within the gap. But there should be some explanation for the pattern of distribution of the chloroplast DNA in the family described by Jansen and Palmer (1987). The inversion cannot be regarded as a parallelism or the result of reversion. The detailed evidence of the DNA sequence offered by Jansen and Palmer precludes such a chance duplication. Jansen (pers comm.) has stated that the DNA segments are too large for transfer whole by viruses or bacteria, a conclusion that I must accept. One other mechanism, however, is possible. Hybridization could have the effect required, and hybridization is a common phenomenon in the Asteraceae where it seems to be a factor in the success of many tribes (Robinson 1983). The chloroplast DNA is transmitted cytoplasmically and is carried only through the female line which prevents any recombination with other cytoplasmic characters, but the maternal limitation does not prevent recombination with various characters transmitted in the nuclear DNA. It seems unavoidable that a chloroplast DNA inversion that starts in one chloroplast of one plant would initially become distributed unevenly in any derived population of sexually reproducing plants. The mixture could easily be perpetuated if the derived plants continued to be as capable of interspecific and even intergeneric hybridization as many present-day Asteraceae. The present assumption is that the more immediate descendents of the earliest Asteraceae with the inverted chloroplast DNA carried the two forms mixed in their populations through many generations, and that the mixture spread across much of the initial diversity of the family. It was from this mixed ancestral population that present Asteraceae were derived, but the older form of DNA was retained in only one subtribe of the comparatively primitive Mutisieae, the Barnadesiinae (Fig. 4).

The conclusions given above accept the primitive nature of the chloroplast DNA in the Barnadesiinae. An interesting question remains as to what other characters of the Barnadesiinae or Mutisieae might also be primitive. No others can be certain. The pollen of Barnadesia, although distinctive and present in the subtribe, is almost certainly not a primitive form. The more typical Mutisian type seen in Chuquiraga and especially Dasyphyllum is more like the Calyceraceae (Skvarla et al. 1977). The lack of an anther appendage in Dasyphyllum also seems highly individual, and is unlike the vaste majority of the

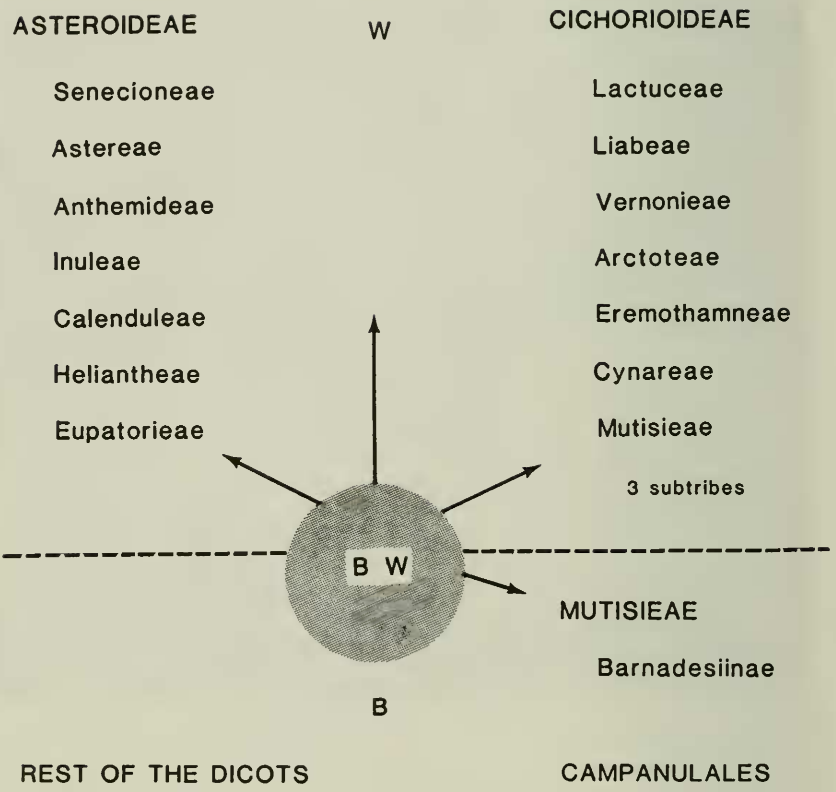

Figure 4. Most probable evolution of variation in chloroplast DNA in Asteraceae. Groups below dashed line (B) with uninverted chloroplast DNA. Tribes above dashed line (W) with inverted chloroplast DNA.

Asteraceae of both presently accepted subfamilies. The appendaged condition seems to represent a condition established in both subfamilies antidating the divergence of the Barbadesiinae. The nonspurred bases of Barnadesia might derive from ancestors that were more like the subfamily Asteroideae before the evolution of the trait in the Cichorioideae. The zygomorphic bilabiate corollas noted by Jeffrey (1977) may be primitive as he has suggested.

One particular set of characters found in the Barnadesiinae and many other Mutisieae offers an interesting possible insight into the early evolution of the Asteraceae. The habits of the Barnadesiinae are notably thorny as reflected in many of their names, Dasyphyllum ferox (Wedd.) Cabrera and Barnadesia horrida Muschler. These plants and some other Mutisieae are also notable for their simple secondary metabolite chemistry compared to that of most other Asteraceae (Zdero et al. 1987). The impression is of a group that relies more on physical defenses instead of chemical ones. These plants are not the rich chemical factories that are seen in so many other tribes of the family. The simple chemistry seems very likely to be a survivor of a more primitive strategy in the Asteraceae.

The simple chemistry of the Barnadesiinae raises one additional possibility. There has been little reason to assume that inversions of DNA sequences of the type seen in the Asteraceae necessarily have any significant benefit. The success of the inverted form in the family, however, might indicate that it is in some way favored. An actual positive benefit might not be involved but there may be a passive ability to better survive and function in a cell that has a richer chemistry. Cronquist (1977) has noted that a plant must be able to withstand its own repellents, and the unique inverted chloroplast DNA of most of the Asteraceae might be better able to withstand the precursors of the numerous poisonous secondary metabolites of most tribes of the family. Even a slight effect could explain the success of the inverted form that is found in all the chemically richer members of the family. It is remotely possible that the more complex chemistry could not have evolved in the family without a less vulnerable inverted form of chloroplast DNA.

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